

A YOUNG *MACRISTIUM* AND THE CTENOTHRISID FISHES

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PRESENTED

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A YOUNG *MACRISTIUM* AND THE CTENOTHRISID FISHES

By N. B. MARSHALL

SYNOPSIS

A young fish, taken by "Discovery Investigations" in the Bay of Biscay, has proved to be the second known representative of *Macristium chavesi* Regan (1903), a species belonging to the order Isospondyli (family Macristiidae). In fin pattern, which is unique among isospondylous fishes gill cover structure, and branchiostegal ray complement, this species is very close to the ctenothrissid fishes of Cretaceous strata.

Consideration of the functional design of the fins of "lower" teleosts with thoracic (or near thoracic) pelvic members suggests that the similarities between *Macristium* and the ctenothrissids are not likely to be due to convergent evolution. *Macristium* would thus appear to be a modern ctenothrissoid fish, a supposition to be fully tested when an adult specimen becomes available.

INTRODUCTION

IN 1903, Mr. C. Tate Regan wrote a short report on some fishes brought back from the Azores by Mr. W. R. Ogilvie Grant. One fish had a quite unusual appearance, but Regan (1903) believed it to be most nearly related to Günther's genus *Bathysaurus*, ". . . which it resembles in the position of the fins and the number of rays, but with the mouth only moderately wide, the dentition weaker, the maxillary dilated posteriorly, the fin rays much prolonged, and the ventrals still more anterior in position." Regan described the fish as a new genus and species, *Macristium chavesi*, and placed it in the family Scopelidae.

When he came to revise the order Iniomi, Regan decided that closer scrutiny of the fish (which was housed in the Ponta Delgada Museum in the Azores), was desirable. Having obtained the fish from Major F. A. Chaves, Regan (1911) revised his judgement of its systematic position. These were his conclusions: "Originally I believed that *Macristium* was related to *Bathysaurus* Günth, which it resembles in the position of the fins and the number of rays. I am now of the opinion that this resemblance is misleading, for I think that in all probability the praemaxillaries would not exclude the maxillaries from the gape. In any case, *Macristium* must be made the type of a distinct family, Macristiidae, probably related to the Alepocephalidae."¹

It is clear, then, that Regan believed *Macristium* to be an isospondylous fish. In his classification of fishes, Berg (1947) puts this genus in the order Clupeiformes (=Isospondyli), suborder Clupeoidei and places it immediately after the superfamily Alepocephaloidea. But he remarks that the systematic position of the Macristiidae is uncertain. This is also Gosline's (1960) view.

¹ Regan continues; "Before returning the fish to the Ponta Delgada Museum it seems best to make a figure of it and to reinforce my original description." But recent correspondence has revealed that the type of *Macristium chavesi* is missing from this Museum.

When working on the Miripinnati (Bertelsen & Marshall, 1956), we were naturally interested in the "lower", soft-rayed teleosts that have large pelvic fins set close to the pectorals. We considered *Macristium* and two Upper Cretaceous families, the Ctenothrissidae and the Chirothricidae, but concluded that the similarities in fin pattern, which are certainly not very striking, could be convergent. (We might also have included *Pantodon*, and would, no doubt, have come to the same conclusion.)

But this survey not only revealed that the Miripinnati are a natural and somewhat isolated group within an "iniomous complex". It led me to realize that there are striking similarities between the fin patterns of *Macristium* and the ctenothrissid fishes, which I discussed when reading a paper (unpublished) on the Miripinnati ("Some new oceanic fishes") to the Challenger Society on 26th October, 1955.

Closer consideration can now be given to these possible, even probable indications of a relationship between *Macristium* and the Ctenothrissidae. Recently when looking through the unnamed *Discovery* Collections, I found a young *Macristium* (taken in the middle part of the Bay of Biscay (Station 2072, 46° 31·6' N., 07° 42·9' W., TYFH, 170 (—0) m., 22. v. 1937). Making due allowance for its immaturity, the form and meristic features of this young fish are close to those of the type specimen (Regan, 1903 : 345 ; 1911 : 204–205). Treatment of these aspects must obviously form the first part of this paper. Then follows an assessment of the affinity between *Macristium* and the ctenothrissids, an enquiry which has involved some consideration of the functional significance of fin pattern in the lower soft-rayed teleosts with thoracic (or near thoracic) pelvic fins.

A young *Macristium chavesi* Regan

(Text-figs. 1–3)

Locality : *Discovery* Station 2072 ; 22. v. 1937 ; 46° 31·6' N., 07° 42·9' W. (middle part of Bay of Biscay) ; TYFH 170 (—0) m.

Standard length of fish, 33·0 mm.; total length, 41·5 mm.

MERISTIC FEATURES

Dorsal rays, 17, the first ray a small splint closely applied to the next ray.

Anal rays, 13, the first ray splint-like.

Pectoral rays (left), 15, the uppermost ray a small splint.

Pelvic rays, 7.

Principal caudal rays, 10 + 9.

(None of the fin-rays is branched.)

Branchiostegal rays, 10.

Gill rakers on first arch, 3 + 1 + 13.

Number of myotomes, 61.

MEASUREMENTS (mm.) and proportions (in parentheses and expressed as percentages of the standard length).

1. *Head*. Length, 6·5 mm. (19·7) ; length of snout, 2·1 (6·4) ; interorbital width, c. 2·0 (6·0) ; horizontal diameter of eye, 1·4 (4·2) ; length of premaxillae, 1·3 (3·9) ; length of maxillae, 2·0 (6·1) ; length of mandible, 3·3 (10·0).

2. *Body* (trunk and tail). Depth of body at origin of pelvic fins, 4.0 (12.1); depth at origin of anal fin, 2.8 (8.5); depth of caudal peduncle, 1.5 (4.5); length of caudal peduncle, 5.5 (16.7).

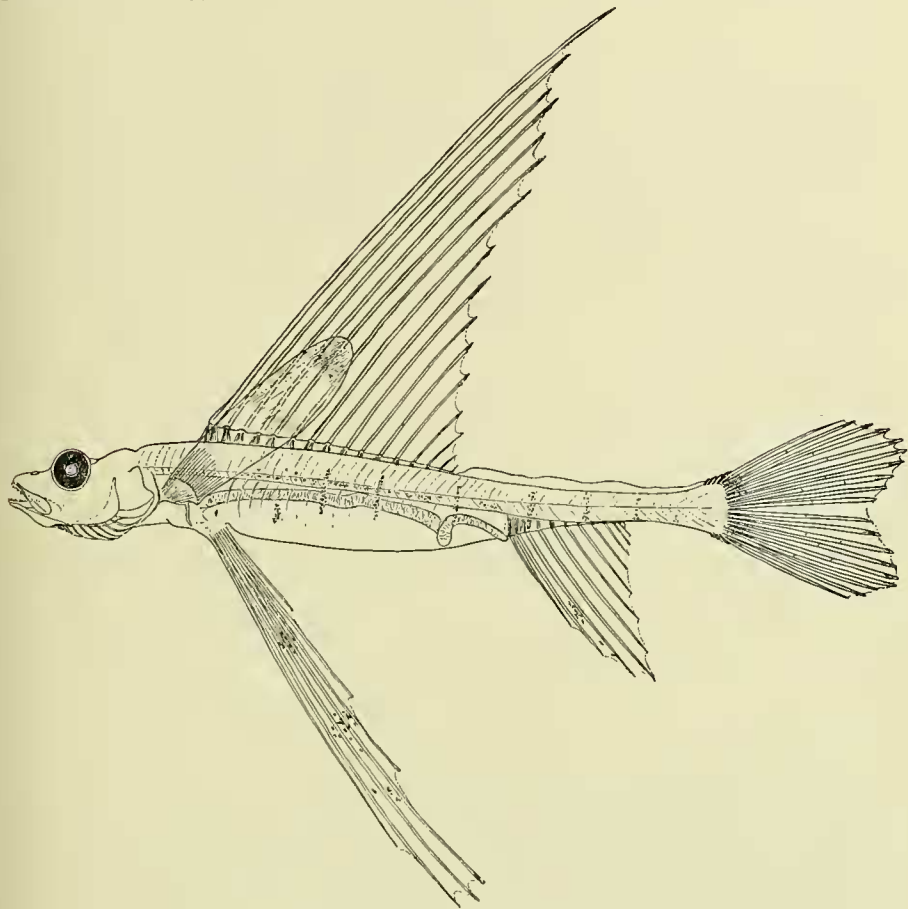


FIG. 1. *Macristium chavesi* Regan. Young fish from *Discovery* Station 2072 ($\times 3\frac{1}{2}$).

3. *Fin positions*. Length between tip of snout and origin of dorsal fin, 10.0 (30.3); snout to origin of anal fin, 23.5 (71.2); snout to origin of pectoral fins, 7.5 (22.7); snout to origin of pelvic fins, 9.0 (27.2).

4. *Fin size*. Length of base of dorsal fin, 12.0 (37.9); length of longest dorsal ray (2nd), 27.0 (81.8); length of base of anal fin, 5.0 (15.2); length of longest anal ray (5th), 9.0 (27.3); length of longest pectoral rays (middle), 10.0 (30.3); length of longest caudal rays, 8.5 (25.8); length of longest pelvic rays (2nd to 4th), 21.0 (63.7).

FIN PATTERN

The most striking features are the high, sail-like dorsal fin and the very extended pelvic fins, which have a thoracic setting (in this young fish there appears to be no attachment of pelvic to pectoral girdle). There is a regular and fairly sharp decrease in the height of the dorsal fin after the longest (2nd) ray, the length of which is about four-fifths of the standard length. The base of the fin extends along the greater part of the trunk region (along rather less than half the combined extent of trunk and tail). The longest rays of the pelvic fins (2nd to 4th) are just over three-quarters the length of the second dorsal ray, and when applied along the body, extend to about the middle of the caudal peduncle. The dorsal and pelvic fins arise at precisely opposite points. A line joining their origins would come just behind the muscular

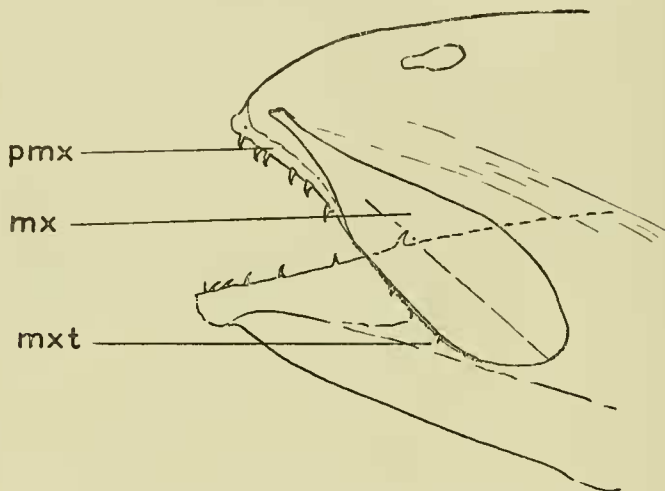


FIG. 2. Jaws of *Discovery Macristium chavesi* ($\times 28$). *pmx*, premaxilla; *mx*, maxilla; *mxt*, maxillary tooth.

bases of the pectoral fins, the rays of which are closely associated, forming relatively long, paddle-shaped fins. The triangular anal fin originates 7 myotomes behind the last dorsal ray, but this separation may be reduced when the dorsal fin is fully formed (see p. 361). The longest rays of the anal and caudal fins are about equal in length and are slightly shorter than the longest pectoral rays.

SCALES

The skin is without any trace of scaling.

JAWS AND DENTITION

The premaxillae and maxillae together form the biting edge of the upper jaw, their contributions being about equal in extent (see Text-fig. 2). The maxillae are paddle-shaped, the greatest width of the blade being about one-third the length of the bone.

They end just before the most forward parts of the eyes. The hinge between the lower jaw and the suspensorium lies vertically under the middle region of the eyes. The width of the jaw at the coronoid process is about one-third the length of the mandible. Upper and lower jaw bones meet in a gape that is directed upwards and makes an angle of about 40° with the long axis of the body.

Teeth are formed on the premaxillae, maxillae, dentaries, vomer, palatines and tongue. They are pointed and recurved and are fairly large compared to the bones that bear them. Each premaxilla has about 6 teeth. There is about the same number of larger recurved teeth forming an inner row on each dentary. The outer row consists of about 10 teeth, which are about half the size of the inner members. A few teeth can just be seen emerging from the dental lamina of each maxilla. The vomer bears 6 teeth (3 on each side), these being slightly larger than the premaxillary teeth. Each palatine carries 3 teeth. The spatulate tongue is armed with a transverse row of 3 pointed, retrorse teeth, which emerge fairly close to the anterior border of this organ.

PSEUDOBANCHIAE

Present.

BRAIN AND SENSE ORGANS

The mid-brain is large compared to the forebrain, which contains the olfactory bulbs. The cerebellum is moderately well developed (Text-fig. 3).

The opening into each nasal sac is a single keyhole-shaped aperture. (As Regan, 1911 definitely states that there are 2 nostrils on either side of the snout, these must be formed at a later stage.)

INTERNAL ORGANS

The intestine is quite straight except for a turn just before the anus (see Text-fig. 1). There is no evidence of a swimbladder.

MUSCULATURE

Except for the uppermost parts of the hypaxial myotomes (which arch over the body cavity) this lower part of the body musculature is quite undeveloped. The lateral and ventral walls of the body cavity are thus perfectly transparent (for the pigmentation is also in a larval condition).

PIGMENTATION

The most conspicuous features are 7 narrow, vertical bars of pigment, 3 being on the trunk and 4 on the tail. The first bar, which does not extend above the horizontal septum, is vertically under the 7th dorsal ray; the second under the 9th, the third under 12th, and the fourth under the last dorsal ray. The fifth pigment bar is opposite the 2nd anal ray, the sixth between the 8th and 9th anal rays, and the seventh is not far behind the last anal ray. There is also a narrow horizontal tract of melanophores running just below the horizontal septum. (It begins just behind the head and ends just before the anus.) There are 3 patches of pigment on the pelvic

fins (see Text-fig. 1) and scattered cells on the webs between the 3rd and 4th anal rays. There is a fine peppering of small melanophores over the bases of the caudal rays.

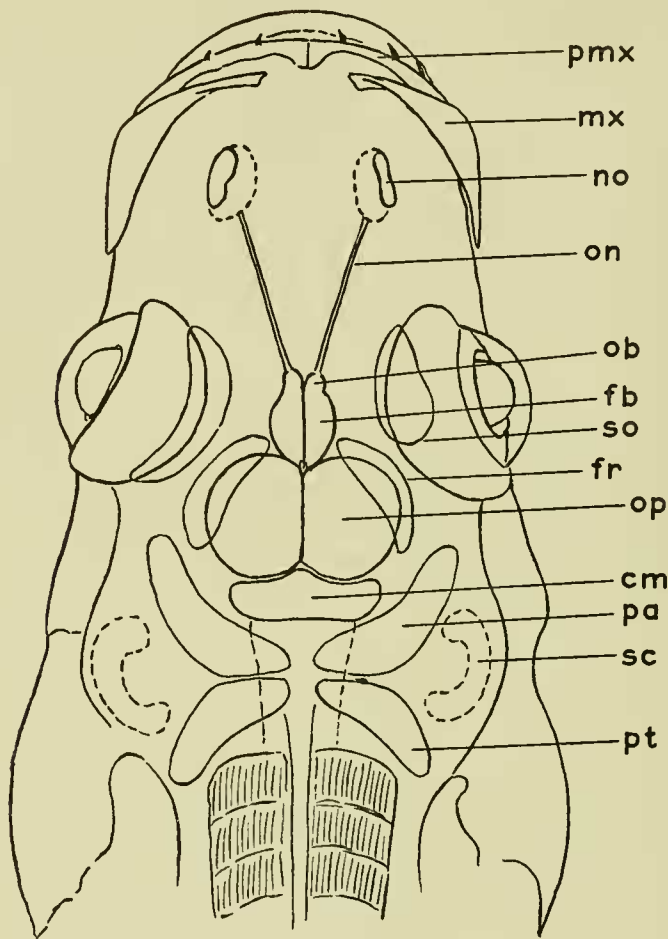


FIG. 3. Dorsal view of head of Discovery *Macristium chavesi* ($\times 21$). *pmx*, premaxilla; *mx*, maxilla; *no*, nostril; *on*, olfactory nerve; *ob*, olfactory bulb; *fb*, forebrain; *so*, supraoccipital bone; *fr*, frontal bone; *op*, optic tectum; *cm*, cerebellum; *pa*, parietal bone; *sc*, semicircular canal; *pt*, post-temporal bone.

Comparison of this description with those given by Regan (1903 and 1911) indicates that this young fish belongs to the genus *Macristium* and, most likely, to the species *chavesi*. Relevant comparative data will be found in Table I.

TABLE I.—*Comparison of Type of Macristium chavesi Regan with Discovery Specimen*

	Type specimen (Regan, 1903 and 1911)	<i>Discovery</i> specimen
Standard length (S.L.) . . .	110 mm.	33 mm.
Fin-ray formula . . .	D. 18; A. 12; Pct. 16; Pv. 8. Principal caudal rays	D. 17; A. 13; Pct. 14; Pv. 7. Principal caudal rays
	10+9	10+9
Number of myotomes . . .	About 62	61
Number of branchiostegal rays . . .	About 8	10
Proportions :		
Depth body into S.L. . . .	$7\frac{1}{2}$	$8\frac{1}{4}$
Length head into S.L. . . .	5	5
Eye diameter into head . . .	Nearly 8	$4\frac{3}{8}$
Interorbital width into head . . .	$3\frac{1}{3}$	c. 3
Base of dorsal fin into S.L. . . .	$2\frac{1}{4}$	$2\frac{3}{4}$
Posterior extent of maxillae . . .	To anterior quarter of eye	To anterior rim of orbit
Origin of anal fin	Just behind last dorsal ray	Well behind (6 myotomes) last dorsal ray

Scrutiny of this Table will reveal that the fin-ray and myotome numbers of the type are quite close to those of the *Discovery* specimen. The one outstanding difference in the proportional data concerns the eye diameter, which is slightly less than one-eighth of the head length in the type and almost equal to one-quarter of this dimension in the *Discovery* fish. However, the type (standard length, 110 mm.) is more than three times as large as the present specimen (S.L., 33 mm.), and it is a general rule that the relative size of the eyes decreases with growth, particularly during the earlier life-history of fishes. Even so, the difference is more than that usually found within any given species.

Reference to Text-fig. 4 will also show that the eyes of the type specimen are set well below the interorbital level (not projecting above, as in the *Discovery* specimen). Yet Regan (1911) states that the frontals are slightly raised above the eyes, which may well be a structural indication of the earlier position and proportionately greater size of these sense organs. If we also consider the damaged, and presumably shrunken, condition of the type specimen, which Regan (1911) thought might have been washed ashore, the divergence between the relative eye sizes seems more comprehensible.

The type specimen of *Macristium chavesi* is also somewhat deeper bodied than the *Discovery* fish and has a relatively longer base to the dorsal fin. This last difference may be coupled with another: according to Regan's (1911) figure the last dorsal ray appears to be no more than one myotome in advance of the first anal ray, whereas in the *Discovery* specimen the separation between these 2 rays is about 6 myotomes. However, Regan (1903) remarks that the anal fin begins "... directly behind the vent, which is slightly posterior to the last dorsal ray." The separation between the last dorsal and the first anal ray may thus be somewhat greater than that shown in his (1911) figure. Furthermore, the last few dorsal rays of the *Discovery* fish are in a very early stage of development, and it may well be that at a later stage the gap between the 2 fins will close. Considerable changes in fin pattern, involving both position and extension of a fin base are not uncommon during the early life-history

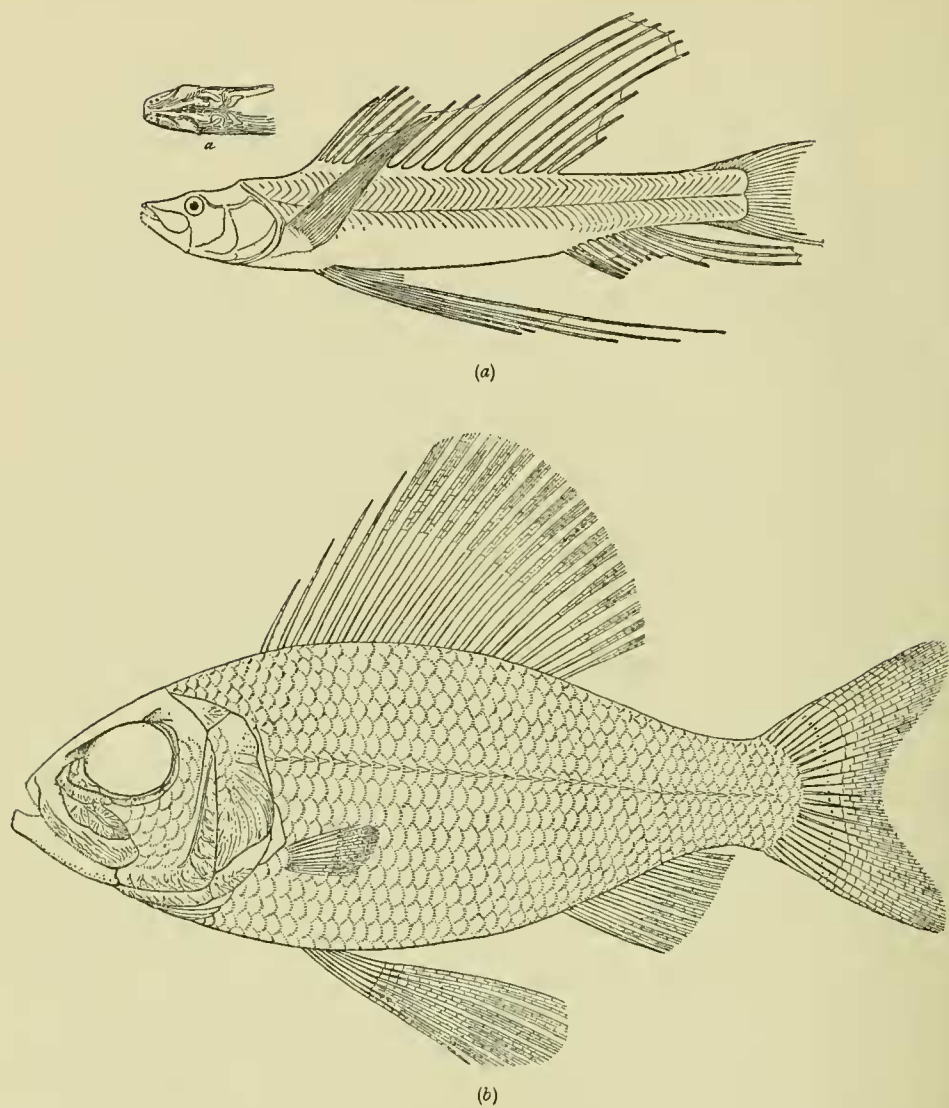


FIG. 4. (a) *Macristium chavesi* Type specimen (from Regan, 1911). Reproduced by kind permission of Taylor & Francis, Ltd. (b) *Ctenothrissa radians* (Agassiz) (from Woodward, 1903). Reproduced by kind permission of the Council of the Palaeontographical Society.

of teleosts. (In the sprat (*Sprattus sprattus*), for instance, the gap between the last dorsal ray and the first anal ray decreases by 3 or 4 myotomes between post-larval and adolescent stages.)

Apart from this dorsal-anal gap, there is very close agreement between the fin position of both fishes (see Text-fig. 4). There are, however, differences in fin form. In the type the posterior parts of the dorsal and anal fins are far better developed than those of the *Discovery* fish. Yet, as already stated, the last few dorsal fin rays, and also the last few anal rays, are in a very early stage of formation. The 5th pelvic ray of the type, which appears to be complete, extends beyond the caudal peduncle, being thus much "in advance" of the corresponding ray of the other fish. But again the difference may be no more than that associated with particular phases of development.

To conclude, having an awareness that the *Discovery* fish is little more than post-larval in phase, there is no good reason for considering it to represent a second species of *Macristium*. When the life-history of *M. chavesi* is adequately known we may expect this young fish to fall into place in the earlier and more active phases, times during which there are trenchant changes in form and function.

MACRISTIUM AND THE CTENOTHRISID FISHES

Despite the thoracic position of their pelvic fins, Woodward (1903), considered the Ctenothrissidae to be closely related to the existing Clupeidae. In his (1901) *Catalogue of the Fossil Fishes in the British Museum (Natural History)*, the synopsis of Cretaceous and Tertiary Isospondyli (p. 5) shows that besides the difference in position of the pelvic fins, the two families can be distinguished in that the abdominal vertebrae of the ctenothrissids lack transverse processes. Reference to the definitions of the families (Ctenothrissidae, p. 119; Clupeidae, p. 128) also reveals that there is some median contact between the parietal bones of the first-named fishes. In the clupeids these two skull bones are completely separated by a well-formed supraoccipital. The outstanding common features of the two families (taken from these definitions) are as follows: "Premaxilla small and maxilla relatively large and loose, both these bones entering the upper border of the mouth; two supramaxillaries; teeth acuminate, but feeble. Opercular apparatus complete, but few branchiostegal rays and no gular plate. Vertebral centra well ossified; ribs nearly or completely encircling the abdominal cavity. Fin fulcra absent. Post-temporal bones in contact with postero-lateral angles of cranium; post-clavicular plate (post-cleithrum) overlapping the clavicle (cleithrum)."

Berg (1947) must have been more impressed by the difference in fin pattern, for in proposing a new suborder Ctenothrissoidei (p. 422) he states that these fishes are "As Clupeidae but with very large ventral fins situated *below the pectorals*" (his italics). This would seem a reasonable proposal, but whatever the opinion, we can at least agree that the ctenothrissids are isospondylous fishes, having soft-rayed fins, a caudal fin with 19 principal rays and an upper jaw bordered by both premaxillae and maxillae. By the same combination of characters, *Macristium* can also be placed in the Isospondyli. Indeed, as already quoted (p. 355) Regan (1911) considered this

genus to be most closely related to the Alepocephalidae, a family that can be reasonably assigned to the suborder Clupeoidea.

Concerning closer comparisons, the most striking resemblance between *Macristium* and the Ctenothrissidae is in fin pattern (see Text-fig. 4). The tall sail-like dorsal fin, extending over the greater part of the trunk; the long, wing-shaped pelvic fins, which arise at points opposite, or nearly opposite to the origin of the dorsal fin; the smaller pectoral fins, set laterally on the shoulders between the lateral line and the base of the pelvics; the rather prominent anal fin, beginning close behind the last dorsal ray and spanning about half the length of the tail; the well-formed shallow-forked caudal fin—these are the outstanding similarities.

This precise form of fin pattern is unique within the order Isospondyli (the nearest, but not very close, approach is with *Pantodon*). Indeed it is almost without parallel among the entire complex of "lower", soft-rayed teleosts (Isospondyli, Ostariophysi, Haplomi, Iniomi, Cetunculi, Miripinnati, Chondobranchii, Giganturoidea and Lyomeri). One striking convergence of fin pattern is with *Bathysaurus*, a congruence that first led Regan (1903) to suspect a relationship between *Macristium* and this genus (now assigned to the order Iniomi, suborder Myctophyoidea, family Bathysauridae). In fact, the *Macristium*-ctenothrissid fin pattern most nearly resembles that of one particular species, *Bathysaurus ferox*. But the term fin pattern, as used by Harris (1953), includes both fin position and fin form. Now the fin positions of *B. ferox* are like those of *Macristium* and *Ctenothrissa* (except that the origin of the dorsal fin is behind the pelvic insertions in the former). In fin form, however, *B. ferox* has less accentuated dorsal and pelvic fins.

There is also a close resemblance between the fin pattern of another iniomous species, *Latropiscus purpurissatus* (Aulopidae) and that of *Macristium* and *Ctenothrissa*. In this aulopid the pelvic fins do arise at points opposite to the origin of the dorsal fin, but again, both kinds of fins are less expansive than those of the two genera in question. The aulopids also have an adipose dorsal fin, which is certainly absent in *Macristium*.

Macristium and *Ctenothrissa* are not only alike in fin pattern, but also in fin-ray numbers, which are listed below in Table II. The figures for *Ctenothrissa* are taken from Woodward (1901 and 1903).

TABLE II.—*Fin-ray Numbers of Macristium chavesi and Ctenothrissa spp.*

Species	Dorsal	Anal	Pectoral	Pelvic
<i>Macristium chavesi</i>	17-18	12-13	16-18	7-8
<i>Ctenothrissa radians</i>	20-25	12+	10-12	7-8
<i>C. vexillifer</i>	18-20	13-14	?	8
<i>C. microcephala</i>	?	c. 10	c. 10	8-9

It will be evident that there is a close correspondence between the numbers of anal and pelvic rays and a fairly near match in dorsal ray complements. There is a bigger gap in the numbers of pectoral rays, but in *Ctenothrissa* the pectorals are rather weakly developed. *Auleolepis*, the other known genus of ctenothrissid fishes, also had small and delicate pectoral fins, each with about 12 rays, while there are 9 rays in the pelvics (Woodward, 1903).

Apart from upper jaws bordered by both the premaxillae and maxillae, there are numerous other similarities between the head structure of *Macristium* and the Ctenothrissidae. The underlying structural congruence is in the markedly forward inclination of the suspensoria. The jaws are thus relatively short, the hinges of the mandible and the ends of the maxillae lying below the orbits. The mandible is not only short but deep, the width at the coronoid process being about a third of the mandibular length in *Macristium* and nearly one-half this dimension in *Ctenothrissa*.

Conforming to the inclination of the suspensoria, the preopercular bones are J-shaped. The divisions between the large opercular and much smaller subopercular bones run backwards and upwards from the angles of the preopercula. The interopercular bones lie below the horizontal preopercular limbs (see Text-fig. 1). There is, in fact, a close correspondence between the gill-cover bone patterns of all three genera, *Macristium*, *Ctenothrissa* and *Aulolepis*. (see also Text-fig. 4).

Macristium and *Ctenothrissa* also have much the same number of branchiostegal rays. Regan (1911) stated that there are about 8 on either side of the type of *Macristium chavesi*: the *Discovery* specimen has 10. In his descriptions of *Ctenothrissa radians*, Woodward (1903: 81) remarks that "the number of branchiostegal rays is uncertain, but there cannot have been less than eight, perhaps ten."

Turning now to differences, the most obvious one is the lack of scales in *Macristium*. In the ctenothrissids the scales are large and regularly arranged, their edges being pectinated in *Ctenothrissa* but smooth in *Aulolepis*. A second striking difference is the development of 2 well-formed supramaxillae in the Ctenothrissidae, whereas in *Macristium* the paddle-shaped maxilla is apparently a single bone. Furthermore, the large blade-like maxillae of the ctenothrissids form two-thirds to three-quarters of the biting edge of the upper jaw, but in the *Discovery Macristium* the fraction is no more than one half. Thirdly, except for the first 4 dorsal rays, the upper pectoral ray, the outer pelvic ray, the 1st anal ray and the outer principal caudal rays, the fin rays of *Ctenothrissa* are branched. In the *Discovery Macristium* none of the fin-rays is branched, and the same appears to be true of the type specimen (Regan, 1911). Lastly there is one appreciable meristic difference. In *Ctenothrissa* and *Aulolepis* the vertebral numbers are from about 30 to 40; in *Macristium* there are about 60.

The significance of these contrasting features can only be properly assessed with an awareness that the *Discovery* and type specimens are young fishes. In both the skull is at an early stage of development (see Text-figs. 3 and 4) and in the former specimen, at least, this is also true of the hypaxial musculature of the trunk region. Regarding the type specimen, Regan (1911) noticed that the abdomen appeared to be very distensible, which either suggests incomplete development of the investing musculature or a poor state of preservation.

Finally, the melanophore pattern of the *Discovery* fish seems to be in a post-larval condition, there being no general pigmentation of the skin, such as appears at metamorphosis.

Considering now the first difference, the complete lack of scales in young *Macristium* need not imply their absence in the adult. In the Scopelarchidae and certain Paralepididae, for instance, the scales do not begin to form until a relatively late stage in

the life-history. At first sight, indeed, young *Macristium* remind one of the *Benthalbella* larvae of scopolarchids. But it is not the absence of scales in relatively large young that provokes the reminiscence, but rather the translucent, muscle-lacking walls of the abdominal cavity. It is reasonable to assume that in fishes with this large type of post-larva the early part of the life-history is prolonged, the rate of differentiation of the organ systems being slow compared to the growth in size. In fact, young *Macristium* may not reach the adolescent stage until they are about 6 inches in length. This could well account for the non-branched condition of the fin rays of the two specimens of *Macristium* (in *Benthalbella* larvae almost all of the fin rays are in this stage of development).

The relatively small (half) share of the maxillae in the biting edge of the upper jaw could also be a larval feature. In just metamorphosed larvae of *Elops*, for instance, this maxillary fraction is between a half and two-thirds, whereas in the adult it is somewhat greater than two-thirds. Could the absence of supramaxillae simply be due to the fact that they have not yet ossified? There is no trace of supramaxillae in the above larvae of *Elops*. If, as seems likely, the early (pre-adolescent) development of *Macristium* is much protracted, the relatively late appearance of certain adult jaw features is by no means impossible. But we can only await the capture of further stages in what is clearly a most interesting kind of life-history.

Lastly, the marked difference in vertebral numbers (about 60 in *Macristium*, 30-40 in the Ctenothrissidae) need not imply marked genetic separation. Instances of a wide range of vertebral numbers *within one family* are not uncommon and, as in the fishes under review, this may be coupled with relatively small variations in the numbers of fin rays. In the Chlorophthalmidae of the Western North Atlantic the fin formula is D. 10-11, A. 7-9, Pct. 15-17, Pv. 8-9, but the vertebrae vary from 38 to 49 (Mead, in the press). There are 45-66 vertebrae in the Scopelosauridae but the usual numbers of rays are: D. 10-12, A. 17-20, Pct. 10-12, Pv. 8-10 (Marshall, in the press).

FIN PATTERNS OF "LOWER" SOFT-RAYED TELEOSTS WITH
THORACIC (OR NEAR THORACIC) PELVIC FINS:
FUNCTIONAL ASPECTS AND CONVERGENCE

Macristium and the Ctenothrissidae are thus closely similar in head structure and fin pattern, the latter being unique within the order Isospondyli. But could these common features be simply due to convergence? More precisely, have these features been independently acquired? And could they be adaptations to a particular way of life? If such questions could be answered in the negative, one could feel more certain of the genetic affinity between the two.

We have already seen that the *Macristium* type of fin pattern is found in two iniomous fishes, *Bathysaurus ferox* and *Latropiscus purpurissatus*. There is also a remarkable resemblance in the numbers of fin rays, which are as follows:

<i>Macristium chavesi</i>	D. 17-18, A. 12-13, Pct. 15-16, Pv. 7-8
<i>Bathysaurus ferox</i> (Type)	D. 18, A. 12, Pct. 14, Pv. 8
<i>Latropiscus purpurissatus</i> (one specimen)	D. 20, A. 12, Pct. 14, Pv. 9

Concerning the two iniomous species, the differences between them, particularly in head structure, are no less striking than the foregoing resemblances. The Bathysauridae and Aulopidae have clearly diverged considerably from their point of common origin, which must be close to the origin (or origins) of the iniomous fishes. Now the fin pattern of most Iniomi suggests that the ancestral fish(es) would have had a short based dorsal fin and abdominal pelvics. If this is so, then the fin array of the two above species could well have been acquired independently (and not be an instance of parallelism). Could the same be true of *Macristium* and *Ctenothrissa*? Before trying to answer this question, some consideration of certain functional aspects of fin pattern in isospondylous and iniomous fishes with thoracic (or near thoracic) pelvic fins will be relevant.

All the members of one suborder of Iniomi, the Alepisauroidea, have abdominal pelvic fins. In the other suborder, the Myctophoidea, only the Myctophidae, the Harpadontidae and the Scopelosauridae can be said to have typically abdominal pelvic fins. In the remaining families, the Aulopidae, the Chlorophthalmidae, the Bathypteroidea, the Ipnopidae, the Bathysauridae and the Synodontidae, these fins are either thoracic in position or inserted well forward on the abdomen, close to the bases of the pectorals. There would thus appear to be a correlation between pelvic fin position and habit. The bathypelagic Iniomi have abdominal pelvics whereas in all but one of the benthic groups (the Harpadontidae), the pelvics have moved near or very near to the pectorals, which have a lateral setting.

In the percoid fishes Harris (1953) has shown that lateral pectoral fins, acting in concert with thoracic pelvics, form an extremely efficient and stable braking system. He also writes: "It is interesting to find that the percoid facies has been evolved at least three times over, since it appears in the Permian Palaeoniscoid, *Dorypterus*, possibly in some Holostei (*Dapedius*) and also in the isospondyl *Ctenothrissa*; all are short, thin, deep-bodied forms where pitching motions would be liable to become excessive during braking if it were not for this pelvic fin migration."

But this disposition of the paired fins is not necessarily an invariable indication of a braking system. Keeping to the Iniomi, the lizard-fishes (Synodontidae) have the habit of lying on the sea floor, propped up by their pelvic fins, which are inserted well forward, between the origins of the pectoral and dorsal fins. A *Trachinocephalus* in just this posture is figured by Ray & Ciampi (1958: 190, fig. 96). As these authors remark (p. 189): "All the lizard fishes are fiercely predatory. They sit on the bottom, resting on their ventral (pelvic) fins until some unsuspecting fish or crustacean swims by. Then they rush so quickly at the prey that the movement can hardly be seen. They prefer sand bottoms but many may be found about reefs and rocks as well as over mud and grass."

"This is one of the groups in which the normal swimming pattern has been altered. For sudden rushes the tail fin is used, but lizard fishes do not often swim when at leisure, preferring to creep about on the bottom on their very large pelvic fins. The pectorals are held out as wings and are probably used as planing devices in their sudden rushes after prey."

Like the Synodontidae and other benthic myctophoids, the Bathypteroidea are without a swimbladder. Having a firmly ossified skeleton and a well-developed

muscular system, they must be denser than their surroundings. And as Houot & Willm (1955) first observed, *Benthosaurus* actually rests on the bottom, supported by its elongated pelvic and caudal rays, which form a tripod.

These supporting rays have a special structure. In the Bathypteroidae the two lowermost, principal caudal rays, which may be much prolonged, are stiffened through being composed of short, closely interlocking, lepidotrichia, these elements being much shorter than those of the other caudal rays. The outermost 2 (or 3) rays of each pelvic fin are also made of very short segments. The same kind of fin-ray modification occurs in the Synodontidae. The two lowermost principal caudal rays are usually comprised of shortened lepidotrichia and certain of the outer pelvic rays also have this special structure (in *Trachinocephalus myops*, the outer 5 pelvic rays; in *Synodus* the outer 4 or 5 rays and in *Saurida* the outer 2 pelvic rays).

All three "legs" of this fin-tripod are thus specially modified, presumably to support the weight of the resting or creeping fish. The other significant feature is that the insertions of the pelvic fins are definitely in advance of the centre of gravity. The tripod rest is thus quite stable, which would not be so if the pelvics were inserted further back along the abdomen (in a typically "abdominal" setting). The forward migration of the pelvic fins would thus seem to be simply related to the formation of a stable undercarriage.

It is clear that the lizard-fishes get a quick take-off from this undercarriage, while observers have seen *Benthosaurus* dart forward from a resting position. Perhaps the raising of the body above the substratum also enhances sensory appreciation of the immediate environment. If, for instance, a fish is flattened against sand or ooze the lower parts of the lateral line system of the head and of the visual field are out of action. The tips of the fin-ray tripod may also give tactile information of local movements of invertebrate food in the deposits.

The other benthic myctophoids, the Aulopidae, Chlorophthalmidae, Ipnopidae and Bathysauridae have also lost the swimbladder. Again, certain of the outer pelvic rays and (usually) the lowermost principal caudal rays are relatively stout and composed of short segments. (In *Aulopus filamentosus* and *Latropiscus purpurissatus* the outer 4 pelvic rays and the 2 lowest caudal rays have this special structure. In *Chlorophthalmus agassizii* and *C. nigripinnis* this applies to the outer 2 or 3 pelvic rays and the lowermost caudal ray, but in *C. punctatus* no single ray of these fins is so differentiated. Concerning *Ipnops murrayi* and *Bathysaurus ferox*, the modification is confined to the pelvic fins, to the outer 3 pelvic rays in the former and to the outer 2 rays in the latter.) Lastly, the pelvic fins of all these fishes are inserted in advance of the centre of gravity.

These fin features are surely close enough to those of lizard-fishes and bathypteroids to suggest that the fishes of the above four families use their pelvic and caudal fins as a mobile tripod-undercarriage.¹ There is no observational evidence to support this view, and indeed, little is known of the biology of these fishes. But the close

¹ It is interesting that the one crossopterygian fish (*Laugia grönlandica*, Stensiö, 1932) with thoracic pelvic fins has specially modified pelvic rays. Like the iniomous fishes described above, some of the pelvic rays are much stouter and composed of shorter lepidotrichia than the other fin rays. Did *Laugia* use its pelvic fins as supports and/or for walking along the bottom?

structural congruence of fin form, to which may be added the common possession of a well-shaped muscular body ending in a forked tail fin, are features suggestive of a darting, synodontid-like habit (based on a "tripod" rest, allowing of a quick take-off).

Aside from these features of fin pattern and form, the benthic myctophoids have few characters in common. Evidently they are not closely related, except perhaps for the Synodontidae and Bathysauridae. In fact, the Chlorophthalmidae are more closely allied to a pelagic family, the Scopelosauridae (Marshall, in the press), than to any of the benthic groups. The similar pelvic and caudal characters of these groups may thus be due to (adaptive) convergent evolution rather than to inheritance from a common ancestor.

As in the Synodontidae, the pelvic fins of the Ctenothrissidae are considerably larger than the pectorals and composed of much stouter rays. Woodward (1903) described the pelvic fins of *Ctenothrissa radians* as follows: "Each of them consists of seven or eight very stout rays all articulated and all, except for the foremost, finely divided in their distal half." If these fins were part of a "percoid" type of braking system, they seem disproportionately large for such a function. But their robust structure may well point to their use as supports when the fish was resting on the bottom. The fact that they have a forward, thoracic setting could then be related to the requirement of an insertion anterior to the centre of gravity. In deep bodied, large-headed fishes, such as *Ctenothrissa* spp., this centre comes close behind the bases of the pectoral fins. In fact, the deeper the body the nearer to the head will be the point of balance. To take an apt example, comparison of *Aulopus filamentosus* with *Latropiscus purpurissatus* reveals that in the former, which is the slimmer bodied, the insertions of the pelvic fins are appreciably behind those of the pectorals. In the deeper bodied *Latropiscus* the pelvics originate just behind the vertical level of the pectoral bases.

Are the adults of *Macristium chavesi* also bottom-living fishes that use their long pelvic fins as two legs of a tripod undercarriage? In the *Discovery* specimen there is no sign of a swimbladder, the lack of which is a particular feature of fishes that spend most of their adult life actually resting on the bottom.

To return to our original question, the foregoing discussion might suggest that the resemblance between the fin patterns of *Macristium* and the ctenothrissids are due to convergent evolution. But our functional analysis of fishes with synodontid-like habits of resting on the bottom simply refers to the paired fins. Nevertheless the striking resemblances between the fin patterns and fin-ray numbers of *Latropiscus purpurissatus* and *Bathysaurus ferox* shows what "Nature can do" by way of convergence. Yet the aulopids and *Bathysaurus* are quite unlike in head structure, whereas *Macristium* and the ctenothrissids have a cluster of head characters in common. The pattern of gill cover bones might, of course, be simply correlated with the forwardly inclined suspension of comparatively small jaws (see p. 365). If so, the convergent features of these fishes would reside in both fin and gill cover pattern.

Against such considerations must be set the correspondence in number of branchiostegal rays and the fact that the *Macristium*-ctenothrissoid fin pattern is unique within the order Isospondyli (p. 364). Furthermore, no single feature or combination of features, precludes the consideration of *Macristium* as a ctenothrissoid fish. The

absence of supramaxillae in *Macristium* seems the most outstanding difference, but these bones may be quite late in ossifying (p. 366). Certainly, the paddle-shaped bone that appears to be the maxilla has a most unusual shape if it is going to be no more than a maxilla.

In conclusion, these problems can only be resolved when an adult *Macristium* becomes available. We shall then know whether each maxilla carries two supramaxillae and whether the parietals meet in the middle line. If the answers are in the affirmative it would seem that *Macristium* can be regarded as a modern survivor of the ctenothrissoid fishes. Meantime the purpose of this paper is to suggest that this outcome is at least possible, perhaps even probable.

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